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Interference competition, the spatial distribution of food and free-living foragers

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Studies of interference competition among foraging animals generally assume that variation in the spatial distribution of food can be neglected. This assumption may be problematic as resource defence experiments suggest that such variation is of the essence in some interference mechanisms. Interpretation of the results of field experiments on this topic, however, is hard because most studies used univariate statistics to analyse multivariate data. Because in free-living foragers interference and patch selection are connected behaviours, treatment effects on these responses are best studied simultaneously, through multivariate analyses. We performed a field experiment in which we provided wild ruddy turnstones, *Arenaria interpres*, with experimental plots that varied in the distance between a fixed number of so-called food pits, and, using multivariate statistics, we studied effects on the combination of the turnstones' behaviour and abundance. We found that when food pits were more spaced out, turnstones were present in higher numbers, while interacting less with each other. Nevertheless, turnstones spent about the same amount of time digging for food, our measure of intake rate, at each interpit distance. These findings imply that to reliably predict the combination of the number, intake rate and aggression of turnstones, the spatial distribution of food has to be known. We would not have reached this conclusion if we had used univariate statistics. In addition, we argue that multivariate statistics helps to clarify the way field experiments on the spatial distribution of food are to be interpreted.

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Keywords: *Arenaria interpres*; field experiment; foraging behaviour; ideal-free-distribution; resource defence; ruddy turnstone

The intake rate of foraging animals is often negatively related to the density of foragers because of competition. Competition is generally thought to arise in either of two ways (Keddy 2001). *Exploitative competition* is the negative effect of others through the removal of resources. As the exploitation of resources is a straightforward process, this type of competition is (presumably) relatively easy to understand. *Interference competition* is the negative effect

of others through direct interactions between individuals. Behaviours underlying interference competition are various and complex (e.g. Huntingford & Turner 1987; Ens & Cayford 1996; Hassell 2000) and understanding of this type of competition is still rudimentary (van der Meer & Ens 1997; Vahl et al. 2005a, b).

Students of interference competition among foraging animals usually study the effects of forager density concurrently with effects of food density (van der Meer & Ens 1997). In this approach it is implicitly assumed that variation in the spatial abundance of resources ('spatial clumping') does not affect the interference process. This may well be problematic. According to literature on resource defence, the 'economically defendability' (Brown 1964) of a given amount of food should decrease with the surface area over which the food is spread (Warner 1980; Grant 1993), as both the movement costs involved with defending a food clump and the number of intruding

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competitors are expected to be higher when the food is spread over a larger area (Davies & Houston 1984). When food is more spread out and with defendability decreasing, the use of aggressive behaviour to acquire resources and the extent to which resources will be monopolized should also be reduced (Grant 1993). Numerous empirical studies have determined the effects of spatial clumping on aggression and resource monopolization; generally (though not unanimously), these studies confirm the resource defence expectations (for a review, see Vahl et al. 2005a).

The effect of spatial clumping on resource defence suggests that the spatial distribution of food has to be considered explicitly in order to arrive at a better understanding of interference competition; variation in the spatial distribution of food may well be of the essence in at least one mechanism underlying interference competition, resource monopolization. Acknowledging variation in the spatial distribution of food may therefore be crucial, especially since natural food distributions generally are not homogeneous (Taylor 1961; Wiens 1976). Unfortunately, neither the literature on interference competition, nor the literature on resource defence provides clear-cut expectations on how the spatial clumping of food should affect the relationship between forager density and intake rate. Some empirical studies, however, shed light on this question. At least four studies (Rubenstein 1981; Theimer 1987; Benkman 1988; Vahl et al. 2005a) have manipulated both the spatial distribution of food and the abundance (i.e., either the number or the density) of foragers to determine effects on aggression and intake rate. These studies found that the spatial clumping of food strongly affected the interference process, but that effects could not be understood without considering variation in the relative social dominance status of the foragers. Theimer (1987) and Vahl et al. (2005a), for instance, found that dominant foragers can better monopolize food that is spatially clumped than food that is dispersed, and that as a consequence, subordinate foragers suffer more from interference competition when food is clumped than when food is dispersed.

The extent to which these findings are important to understand the behaviour of free-living animals foraging under natural conditions is still an open question, because the four studies mentioned above were all conducted in the laboratory, using captive foragers. The most direct approach to study whether interference effects among free-living foragers depend on the spatial distribution of food would involve manipulation of both the spatial distribution of food and the density of wild foragers (Vahl et al. 2005b). Manipulating the density of free-living foragers, however, is very difficult and we are not aware of any study that has attempted to do so. Therefore, the most relevant data to date come from studies that have manipulated the spatial distribution of food in the field, but not the density of foraging animals. Several such experiments have been performed (Table 1). Quite consistently, these studies found that with increasing plot size (1) the number of foragers increased, whereas forager density decreased and (2) aggression decreased (see Table 1). With regard to the correlations between forager abundance and intake rate or aggression, and with regard to effects

of plot size on intake rate and aggression after correction for variation in forager abundance, the studies were less consistent (Table 1).

Unfortunately, interpretation of these results is not straightforward. What complicates matters is that most studies analysed treatment effects on the abundance of foragers, their intake rate and their aggression separately. Effects on these responses, however, are best studied simultaneously, because in free-living foragers, interference and patch selection are connected behaviours. In response to changes in aggression and intake rate, for instance, foragers may adjust their distribution over food patches. To study treatment effects on these three responses simultaneously, requires the use of multivariate statistics (Stevens 1996).

To solve these interpretational problems, the field experiments could be reanalysed. Rather than doing so, we performed a new field experiment to describe effects of the spatial distribution of food on free-living foragers, and we used multivariate analyses to analyse these effects. In this experiment, we provided wild birds with experimental plots in their usual foraging area, and we manipulated the distribution of food by varying the distance between a fixed number of regularly distributed food pits. We recorded the responses of visiting ruddy turnstones, *Arenaria interpres* (henceforth called turnstones), a species that we previously used to address the same question in laboratory experiments on captive foragers (Vahl et al. 2005a; Vahl & Kingma, in press). In the discussion, we examine whether the use of univariate statistics would have affected our results, and we reflect on the advantages of using multivariate statistics to analyse field experiments on the spatial distribution of food.

METHODS

We designed our experiment according to a randomized block design: we studied the effect of one treatment factor, the distance between food pits ('interpit distance'), with three levels (10, 20 and 30 cm) and we blocked our observations in groups of three trials (we refer to these blocks as 'triplets') to minimize variation due to measurements at different moments in time. The experiment consisted of 10 triplets, each containing all three interpit distances once (in random order). There was one missing value and hence we had 29 data points.

We studied treatment effects on three response variables: the number, intake rate and the amount of aggressive behaviour of turnstones. As plot size varied between treatments, the density of turnstones did not have a one-to-one relationship with the number of turnstones. Moreover, the experimental plots did attract not only turnstones, but also sanderlings, *Calidris alba*, red knots, *Calidris canutus*, laughing gulls, *Larus atricilla*, herring gulls, *Larus argentatus*, ring-billed gulls, *Larus delawarensis* and starlings, *Sturnus vulgaris*. To see whether conclusions would be different if measures of abundance other than the number of turnstones were used, we repeated all analyses using (1) the density of turnstones (number/m²), (2) the biomass (kg), or (3) the biomass density (kg/m²) of

Table 1. Field experiments on the effect of the plot size (X) on the abundance (Y_1), the foraging success (Y_2) and the frequency of (per-capita) agonistic behaviour (Y_3) of free-living foragers*

						Main effects			Correlations					Corrected effects			References					
						Size of experiment			XY ₁		XY ₂	XY ₃	Y ₁ Y ₂		Y ₁ Y ₃			XY ₂ Y ₁		XY ₃ Y ₁		
									Y _{1,n}	Y _{1,d}			Y ₁	Y _{1,n}	Y _{1,d}	Y _{1,n}		Y _{1,d}	Y ₁	Y _{1,n}	Y _{1,d}	Y _{1,n}
Species	English name	n ₁	n ₂	Food	Surface area																	
Birds	<i>Junco hyemalis</i>	Dark-eyed junco	2	u	Amount	Variable	(+)	(-)														
	<i>Passer domesticus</i>	House sparrow	2	u	Neither	Variable			(+)	-	0,-											
	<i>Passer domesticus</i>	House sparrow	7	35	Density	Variable	+	-			-	+										
	<i>Passer domesticus</i>	House sparrow	2	26	Density	Variable	(+)		0	0	-	+0,-										
	<i>Turdus merula</i>	European blackbird	2	498	Density	Variable						-										
	<i>Zenaida aurita</i>	Zenaida dove	2	24	Amount	Constant			+		0,-											
—	Several passerines†	2	24	Amount	Constant			+														
Mammals	<i>Lepus europaeus</i>	European hare	2	28	Amount	Constant					(-)			+0,-								

*The column 'size of experiment' indicates the number of levels of plot size (n_1), and the total number of trials performed (n_2). For some studies, the latter aspect is unknown (u). The column 'food' indicates whether the amount or the density of food was kept constant, or neither of them. The column surface area indicates whether or not the surface area over which forager abundance was expressed was constant; in the former case, effects on the number and the density cannot be distinguished (Y_1), whereas in the latter case, the number ($Y_{1,n}$) and the density ($Y_{1,d}$) of foragers are uncoupled. In the 'main effects' column, the 'correlations' column and in the 'corrected effects' column, it is indicated whether the relationship or the correlation between two variables was negative (-), positive (+), absent (0), dome-shaped (d) or cubic (c). Signs within brackets are not given by the original author(s), but are deduced by us. The correlation between forager abundance and aggression in the study of Goldberg et al. (2001) depended on the temporal predictability of food patches; the correlations between forager abundance and intake rate and aggression in the study of Monaghan & Metcalfe (1985) depended strongly on the dominance status of foragers. All other multiple effects depended on plot size.

†Included in the analyses were northern red cardinals, *Cardinalis cardinalis*, field sparrows, *Spizella pusilla* and white-throated sparrows, *Zonotrichia albicollis*.

all species present on the experimental plot as the measure of abundance.

Study System and Subjects

The experiment was conducted at one of the beaches of Delaware Bay, U.S.A., on 5 days between 24 and 30 May 2003. Delaware Bay is one of the most important spring stopover sites for shorebirds along the east coast of North America (Clark et al. 1993). Turnstones are among the most abundant species in the bay, with peak counts of over 100 000 individuals (Clark et al. 1993). The main food source for turnstones foraging in this bay are the eggs of horseshoe crabs, *Limulus polyphemus* (Tsipoura & Burger 1999). Turnstones forage on loose eggs that are brought to the beach surface by the reworking of waves, tides, and bioturbation of horseshoe crabs and other fauna (Kraeuter & Fegley 1994; Sherman et al. 1994) but they are also able to dig up clusters of eggs buried in the sand (Sullivan 1986; Tsipoura & Burger 1999). In doing so, they attract individuals of several other species (Myers et al. 1979) that cannot reach buried eggs themselves. In 2003, the amount of food on the beaches was relatively low (Smith & Bennet 2004) and turnstones got crab eggs mainly by digging for them in the sediment.

Study Site and Experimental Set-up

The experiment was performed at one beach in the village Reed's Beach, Cape May County, NJ. This beach is quite small (depth \times width: 10 \times 90 m). It is unique in that it is enclosed by 2-m-high walls on all but the bay-side. Hence, the beach has a basin-like appearance. Since this beach was completely flooded at high tide, and since at low tide the birds would be far out on the mudflats, we conducted all trials at incoming or outgoing tides ($\bar{X} \pm \text{SD} = 2.32 \pm 0.33$ h before and 1.34 ± 0.46 h after high tide). Triplets took 45 min at most ($\bar{X} \pm \text{SD} = 34.6 \pm 5.3$ min).

In each trial we created one experimental plot at approximately 3 m from the water line. To mark experimental plots for the observers, we placed black stones, which were abundant on the beach, on their corners. Each plot contained 25 food pits, positioned in a regular 5 \times 5 grid. Food pits were holes of approximately fixed size and cylindrical shape; we created them by pressing a film canister in the sand (diameter 31 mm, depth 51 mm). In each pit, we placed a spoonful of crab eggs ($\bar{X} \pm \text{SD} = 4.2 \pm 0.7$ g, $N = 50$), corresponding to approximately 750 eggs (1 g of eggs = 183.1 ± 16.3 eggs; based on nine egg counts), and a thin layer of sand (5.7 ± 0.2 ml, $N = 10$) to cover the eggs. The upper 4 cm of each pit was left empty so that foragers could easily see the food pits. Eggs used in the experimental trials were isolated from sediment samples by elutriation, and had been stored at 4°C for at most 1 day. The experimental food pits resembled the pits turnstones dug themselves to reach buried egg clusters, both in size (depth 51.3 ± 7.4 mm, $N = 16$) and shape, and turnstones were eager to forage in them. Importantly, food at the experimental

plot was abundant and easy to gather relative to food in the direct neighbourhood of the experimental plot (as was also clear from the strong preference of foragers for the experimental plots).

Between trials we experimentally varied the distance between food pits. The smaller two experimental interpit distances (10 and 20 cm) fell below the size range of turnstones (length 210–255 mm; Hayman et al. 1986). Nevertheless, monopolization of multiple food pits required the turnstones to move actively between food pits at each of the three interpit distances. While varying the distance between food pits, we kept constant the number of food pits per plot and the number of eggs per food pit. Consequently, the size of the experimental plot (0.25, 1.00 or 2.25 m²) and the density of food pits (100, 25 or 11 number/m²) varied concurrently with interpit distance. We think that the simultaneous variation of several aspects of the distribution of food is inevitable in experiments on the effect of the spatial distribution of food.

During each trial we recorded the behaviour of birds on the experimental plot with a video camera (Sony dcr-trv 900e) positioned on the veranda of one of the elevated houses bordering the beach. Experimental plots were only 20–30 m away from the camera. Although birds that foraged on the experimental plot could see the observer and the camera, this did not seem to affect them, probably because they were used to people, and because the observers were not actually on the beach.

Experimental Procedure

The same two observers (W.K.V. and K.M.) conducted all trials together. To create an experimental plot, one observer set foot on the beach from the site opposite to that of the camera. In doing so, he necessarily disturbed the birds foraging on the beach, which readily took off for another beach. However, new birds would arrive even before the observer had left the beach, and the first birds generally started to feed on the experimental plot within the first minute after preparation. Video recording started when the first turnstone entered the experimental plot and lasted for 5 min. Trials in which (at any moment) more than three laughing gulls, and/or more than one herring gull or ring-billed gull were present were excluded from the experiment.

Video Analysis and Recorded Behaviour

We analysed our video recordings at one-fifth of normal speed, using The Observer 4.1 Event Recorder (Noldus Information Technology, Wageningen, The Netherlands). To minimize start-effects, such as a gradual rise in the number of foragers, we discarded the first 60 s of each record. To limit effects of resource depletion, digestive constraints and satiation, we additionally discarded the last 60 s of each record. Thus, we restricted all analyses to a 180-s time span. Because of an external disturbance one trial lasted for about only 220 s. After exclusion of the first 60 s, we therefore had only a 160-s interval for

analysis. We extrapolated response variables for this trial by multiplying all events with a factor 180/160.

We calculated the abundance (either the number or the density) of foragers as the average of 5-s interval counts of the number of individuals per species on the experimental plot. Collective biomass was estimated by summing for all species the product of the average number of individuals (Table 2) and the median body mass of an individual (sanderling: 71.5 g; turnstone: 137.0 g; red knot: 152.5 g; laughing gull: 320.0 g; big gull: 802.5 g; mass values from del Hoyo et al. 1996, and starling: 82.5 g; Feare 1984). Note that we grouped herring gulls and ring-billed gulls in the category 'big gulls', because our subjective observations suggest that the two species had the same effect on turnstones.

To determine intake rate and aggression, we recorded the behaviour of focal turnstones. As focal individual we chose the turnstone closest to the centre of the experimental plot. When a focal turnstone left the experimental plot, we continued the analysis by recording the behaviour of a new focal bird. We approximated intake rate by measuring the time spent digging in the food pits (%); when 'digging', turnstones were actively routing with their bill through the sand. We could not measure intake rate directly because plot size restricted the extent to which we could zoom in on the turnstones. However, digging time and intake rate (the number of swallowing movements) were strongly correlated ($R^2 = 0.91$, $F_{1,67} = 641.7$, $P < 0.01$) in an observational data set gathered on nearby beaches by systematically recording the behaviour of foraging turnstones for 60 s ($N = 68$). We measured aggression as the number of intraspecific agonistic interactions that focal turnstones performed per trial (number/180 s). Interactions comprised 'fighting', 'attacking', 'threatening', 'avoiding' or 'escaping' (for a detailed description of the latter four interaction behaviours: see Vahl et al. 2005b). In analyses based on all species, aggression was measured as the rate of all (intra- and interspecific) interactions performed by focal turnstones.

Data Transformation and Hypothesis Testing

We analysed our data using the General Linear Model procedure in SYSTAT 10 (SPSS, Inc., Chicago, IL, U.S.A.), treating both 'triplet' and 'interpit distance' as categorical

Table 2. The number of individuals per species observed on the experimental plot

Species	Interpit distance (cm)		
	10	20	30
Turnstone	2.9 (1.3, 4.9)	9.4 (1.6, 11.5)	12.1 (4.5, 20.9)
Sanderling	2.0 (1.9, 4.9)	3.8 (2.8, 7.6)	8.3 (8.2, 21.1)
Red knot	0.1 (0.1, 0.3)	0.1 (0.4, 1.2)	0.2 (0.4, 1.4)
Laughing gull	0.4 (0.4, 0.9)	0.5 (0.5, 1.4)	0.6 (0.9, 2.2)
'Big gulls'	0.1 (0.1, 0.3)	0.0 (0.1, 0.2)	0.0 (0.1, 0.3)
Starling	0.1 (0.1, 0.3)	0.1 (0.1, 0.4)	0.2 (0.3, 0.7)

Given are the averages per treatment with the associated standard deviations and maxima in brackets.

factors. This procedure is able to handle missing values. In all graphs that include information on triplets, we replaced the missing value with the associated treatment average. In the analyses, we did not replace the missing value. To study the effects of our treatment factor, we ran a Multivariate analysis of variance (MANOVA) on the combination of the three response variables: the number of turnstones, the time spent digging and the rate of intraspecific interactions. We repeated this analysis thrice, using the density of turnstones, the biomass of all species or the biomass density of all species as measure of abundance. We log transformed all response variables (Vahl et al. 2005a, b). In each of the four MANOVAs, we used a 0.01 significance level. This implies that the overall experiment-wise error rate did not exceed 0.04. We judged assumptions of normality and homoscedasticity by visually inspecting probability plots (Miller 1997).

RESULTS

The distance between food pits had a significant effect on the combination of the number of turnstones on the experimental plots, their intake rate, and their aggression (Table 3). There was almost no overlap between the combination of the three response variables at the three interpit distances, as is clear from both the multivariate representation, the three clouds of points were clearly separated (Fig. 1a), and from the strong correlation between the interpit distance and the first canonical variate (Table 3). The most pronounced effect was on the combination of the number of turnstones and their aggression (Fig. 1d), and on the combination of the number of turnstones and their intake rate (Fig. 1b); the combination of aggression and intake rate was not so much affected (Fig. 1c). The combination of response variables at the smallest interpit distance differed mainly from that at the two larger interpit distances in that fewer turnstones were present at the smallest interpit distance (Fig. 1a, d and g). The combination of response variables, however, also differed between the two larger interpit distances; when food pits were 20 cm apart, turnstones were present in slightly lower numbers than when food pits were 30 cm apart, but they interacted more with each other (Fig. 1a, d and f).

The effect of interpit distance on the combination of response variables is furthermore apparent from the correlations among the responses variables (Table 4). Especially, the correlation between the number of turnstones and the rate of agonistic interactions depended much on whether variation in interpit distance is acknowledged. Overall, that is, when variation in interpit distance is neglected, the number of turnstones was uncorrelated with the rate of agonistic interactions. When variation in interpit distance is acknowledged, however, there was a rather tight, positive association between the number of turnstones and aggression (Fig. 1d).

Turnstone Density

Even though turnstones were present in higher numbers when the distance between food pits was larger, their

Table 3. The effect of interpit distance (X) on the number of foragers (Y_1), the percentage of time turnstones spent digging (Y_2) and the rate of agonistic interactions (Y_3)

	Multivariate ANOVA					Canonical correlation analysis						
	Y_1, Y_2, Y_3					Correlations				Loadings		
	df	Value*	F	P	X	r	χ^2	df	P	Y_1	Y_2	Y_3
Triplet	27, 44	0.19	1.2	0.25	Variate 1	0.97	76.3	6	<0.01	-0.70	-0.17	0.08
Interpit distance (X)	6, 30	0.05	18.0	<0.01	Variate 2	0.46	5.9	2	>0.05			

Given are MANOVA results, the canonical correlations regarding interpit distance (X), and the associated canonical loadings, all concerning log-transformed data. Effects significant at the 0.01 level are indicated by bold P values. The MANOVA results indicate that the combination of the three (log-transformed) response variables differs significantly between the three interpit distances, but not between the 10 triplets. The canonical correlation analysis gives the correlation (r) between interpit distance (X) and two canonical variates, which are compound variables formed by the linear combination of response variables that results in the greatest amount of among-group to within-group variation. Interpit distance is strongly and significantly correlated with the first canonical variate, but not with the second. The canonical loadings indicate the correlation between the first canonical variate and each of the three response variables; as it turns out, it is the number of turnstones (Y_1) that is most closely aligned with the first canonical variate.

*Test statistic given is Wilks' lambda (Harris 1975); other multivariate statistics led to identical conclusions.

density was lower at this condition. Effects on the number and the density of turnstones could be different because the distance between food pits also affected the size of experimental plots; the surface area of experimental plots was nine times larger when food pits were far apart than when food pits were close together. Nevertheless, analyses based on the density of turnstones yielded qualitatively the same results as analyses based on the number of turnstones: interpit distance had a strong ($r = 0.89$) and significant effect on the combination of the three response variables (Wilks' lambda = 0.17, $F_{6,30} = 7.1$, $P < 0.01$). The main difference between the three interpit distances was in the combination of turnstone density and intake rate and in the combination of turnstone density and aggression: when food pits were 30 cm apart, turnstone density was about half of that at the two smaller interpit distances (Fig. 2b), whereas intake rate was somewhat higher and aggression lower than at the two smaller interpit distances. Turnstone density did not differ significantly between the 10- and the 20-cm treatment, suggesting that the increase in the number of turnstones between these two treatment levels was proportional to the corresponding increase in plot size.

All Species

Effects of interpit distance on the biomass and the biomass density of the individuals of all species together were similar to effects on the number and density of turnstones (Fig. 2). With increasing distance between the food pits, the biomass of all species together increased (Fig. 2c), but not so much as to be proportional to the increase in plot size; therefore, the biomass density of all species together decreased with interpit distance (Fig. 2d). Effects on the rate of intra- and interspecific interactions together were also similar to those on the rate of intraspecific interactions alone (Fig. 3). Even though the number of individuals of species other than turnstones was substantial, most interactions of focal turnstones were directed at conspecifics; at all three interpit

distances, the rate of interspecific interactions (Fig. 3b) was much lower than the rate of intraspecific interactions (Fig. 3a). Most interspecific interactions comprised of attacks and threats towards the many sanderlings that tried to share the food pit owned by the focal forager, and escapes and avoidances from the occasional gull that was attracted by the experimental plot. Statistically, treatment effects on biomass and biomass density were also highly comparable with those on the number and the density of turnstones, respectively.

DISCUSSION

The spatial distribution of food strongly affected the behaviour and success of the free-living foragers participating in our experiment. Multivariate analysis showed that it was the combination of, especially, the number of turnstones and their aggressive behaviour that depended on the spatial distribution of food. Inspection of the correlation coefficients also revealed that the correlation between the number of turnstones and both their intake rate and their aggressive behaviour depended on the distance between food pits. The immediate lesson that can be drawn from this finding is that there was not a one-to-one relationship between the amount of food and the combination of the three response variables: the same amount of food yielded a different combination of the three response variables, depending on the spatial distribution of the food. This implies that to reliably predict the number, intake rate and aggressive behaviour of turnstones, the spatial distribution of food has to be known. Additionally, these findings imply that the pressure exerted by turnstones on their prey varied with the distance between food pits: when food was spaced out, the product of intake rate and the number of foragers (the 'foraging pressure') was higher (Fig. 4). This illustrates the idea that reduced predation pressure as a result of increased predator interference may be an important advantage of clumping to prey, as was pointed out by Taylor (1977). Although clearly outside the scope of this study,

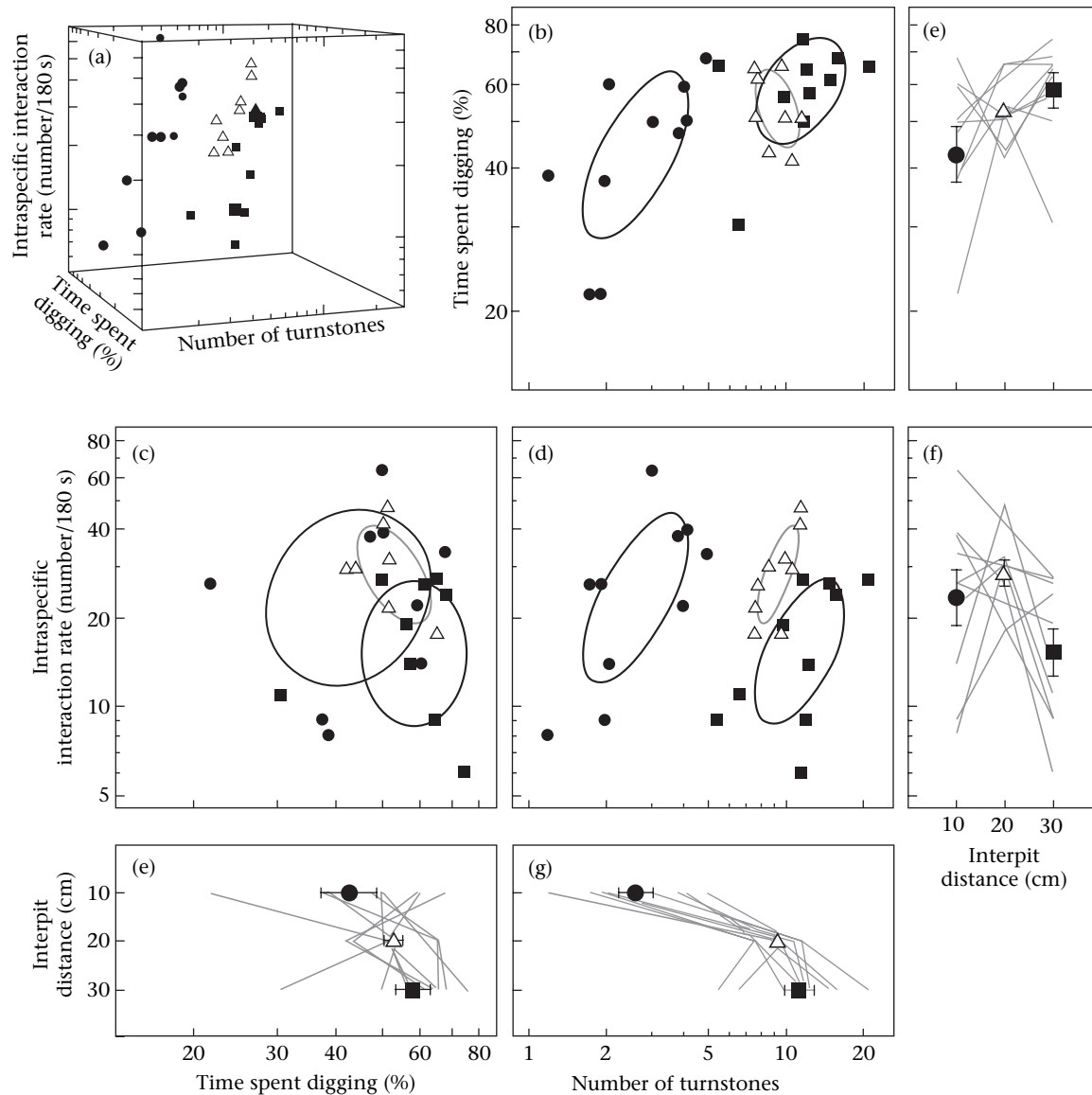


Figure 1. Effects of the distance between food pits on the three response variables: the number of turnstones, the time spent digging (our measure of intake rate) and aggression. In all panels, symbols (circles, triangles and squares) indicate interpit distance (10, 20 and 30 cm, respectively). (a) Three-dimensional relationship between the three response variables. (b–d) and (e–g) give the two- and one-dimensional projections of this three-dimensional relationship, respectively. Note that panel (e) features twice. (a–d) Symbols represent averages per trial. (b–d) Ellipses indicate the 95% confidence intervals of the mean for each interpit distance (grey confidence intervals represent the intermediate treatment level). (e–g) Symbols represent averages per treatment level, and error bars indicate one standard error of the treatment averages. The thin grey lines connect observations within triplets; they represent the 10 blocks of our randomized block design.

this suggests that the small-scale distribution of food may ultimately affect the dynamics of both predators and their prey.

While the number of turnstones increased with interpit distance, the density of turnstones decreased. This shows that the relationship between the number of foragers and surface area is not one-to-one either: just as the relationship between the number of foragers and the amount of food, this relationship depends on the spatial distribution of food. Even though interpit distance affected the number and the density of turnstones differently, the general conclusion to be drawn from tests that use either the number or the density of turnstones as measure of

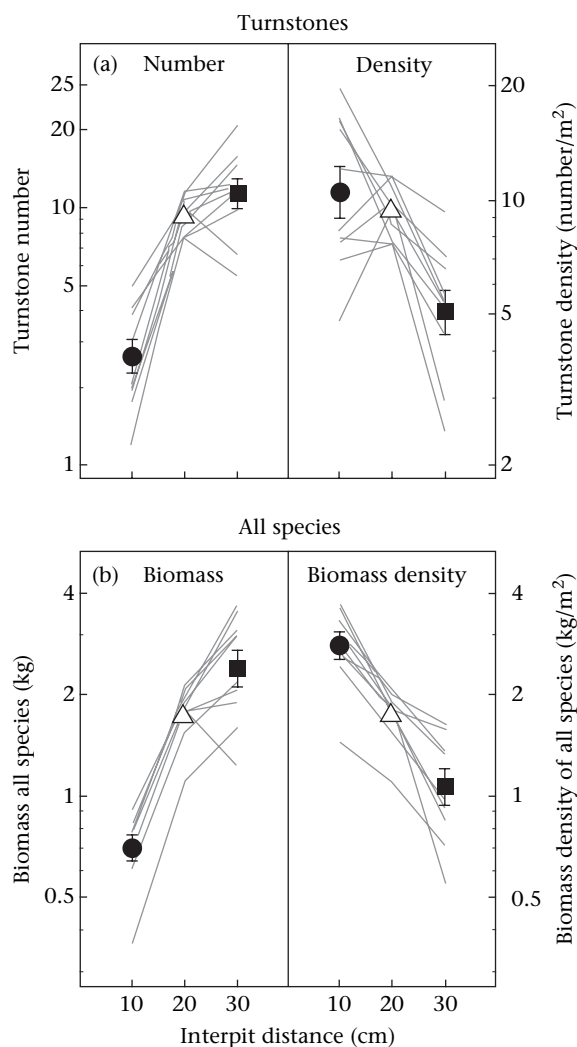
abundance is the same: the combination of the abundance, intake rate and aggression of free-living foragers depended on the spatial distribution of food. In fact, the same general conclusion is reached from tests that use the biomass or the biomass density of all species on the experimental plot as measure of abundance.

As plot size, food density and interpit distance varied concurrently, we cannot determine to which of these three aspects of the food distribution the foragers responded. Although this may seem as a flaw in the experimental design, we think that simultaneous variation of various aspects of the distribution of food is inevitable. Indeed, in all field experiments on the effect

Table 4. Correlations among the three (log-transformed) response variables; the number of turnstones (Y_1), the time spent digging (Y_2), and the intraspecific interaction rate (Y_3)

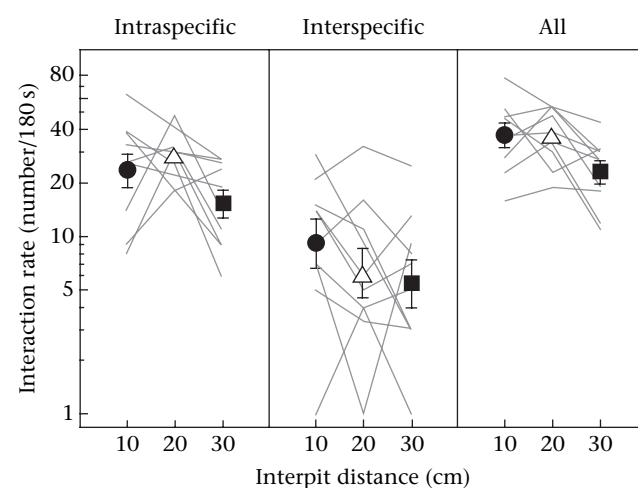
Pair	(Partial) correlation coefficients							
	Simple		First order				Second order	
	Set	r_s	Set	r_s	Set	r_s	Set	r_s
$Y_1 Y_2$	{—}	0.59	{X}	0.50	{Triplet}	0.61	{Triplet, X}	0.36
$Y_1 Y_3$	{—}	0.13	{X}	0.65	{Triplet}	−0.04	{Triplet, X}	0.61
$Y_2 Y_3$	{—}	−0.09	{X}	0.01	{Triplet}	−0.19	{Triplet, X}	−0.03

For each pair of response variables, the simple (unconditioned) correlation coefficients are given, as well as the first, and second order correlation coefficients conditioned on the block factor triplet, the distance between food pits (X), or both (as indicated by the set of variables given within braces). The effect of the distance between food pits on the correlations between the response variables can be studied in two ways: (1) simple correlations can be compared with first order partial correlations conditioned on the distance between food pits, and (2) first order partial correlations conditioned on the block factor triplet can be compared with the second order partial correlations conditioned on both the block factor triplet and the distance between food pits.

**Figure 2.** The effect of the distance between food pits on (a) the number and the density of turnstones, and on (b) the biomass and the biomass density of individuals of all species on the experimental plot. Symbols represent averages per interpit distance, error bars represent one standard error of these averages, and thin grey lines connect observations within triplets and represent the 10 blocks. Note that panel (a) corresponds to Fig. 1g.

of the spatial distribution of food, several aspects of the distribution of food varied concurrently. We think that effects of the various aspects of food distribution can only be disentangled by performing a sequence of experiments that vary in the aspects of food distribution that are simultaneously manipulated. Meanwhile, we need to be careful in attribution treatment effects to specific aspects of the food distribution, and we need to take into account the subtle differences between experiments when comparing experiments.

A possible interpretation of treatment effects on the number of turnstones and their intake rate is provided by the basic ideal-free-distribution model (Fretwell & Lucas 1970), modified so as to apply to foraging animals that have to choose between food patches (Sutherland 1983). This model predicts that foragers will distribute themselves over patches of different quality in such a way

**Figure 3.** The effect of the distance between food pits on the rate of intraspecific interactions, the rate of interspecific interactions, and the rate of all (intra- and interspecific) interactions. Symbols represent averages per interpit distance, error bars represent one standard error of these averages, and thin grey lines connect observations within triplets and represent the 10 blocks. Note that the left panel corresponds to Fig. 1f, but that the ordinate has a different range.

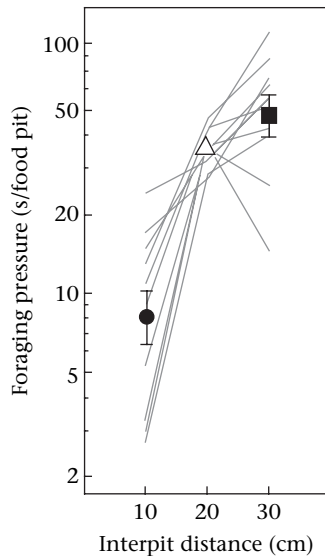


Figure 4. The estimated foraging pressure per interpit distance. Foraging pressure was calculated as the product of the average number of turnstones and the time spent digging per trial. Symbols represent averages per interpit distance, error bars represent one standard error of these averages, and thin grey lines connect observations within triplets and represent the 10 blocks.

that the same intake rate is achieved in each occupied patch, with better patches harbouring more foragers (the model does not generate explicit predictions on the rate of agonistic interactions). Applying this model to explain our experimental results may seem problematic, because within each trial foragers could only choose between foraging on the experimental plot or somewhere else in the environment. However, assuming that the quality of the environment stayed constant throughout triplets, the ideal-free-distribution model can be invoked to explain treatment effects within *triplets*. If patch quality increased with interpit distance, the finding that more foragers were present at the higher interpit distances, whereas intake rate was about the same at each interpit distance, would be in line with the predictions of the ideal-free-distribution model.

Added Value of the Multivariate Analysis

Our analysis differed from that of previous field experiments on the effect of the spatial distribution of food (Table 1) in that we used multivariate statistics. We think use of multivariate statistics clarified the interpretation of our results in several ways.

First, by using multivariate analyses we were able to detect treatment effects on the *combination* of response variables (Stevens 1996); we found that interpit distance especially affected the combination of the number of foragers and their aggression. Had we used (univariate) analyses of variance (ANOVAs) to test for treatment effects on each of the three response variables separately, it would not have been possible to detect this effect on the combination of response variables. Instead, we would have concluded that the distance between food pits had

a significant main effect only on the number of turnstones on the experimental plot, and not on their intake rate, nor on their aggression (for a reanalysis of our data with ANOVAs, see Appendix). Thus, use of ANOVAs would have led us to believe that the spatial distribution of food can be neglected in studies of intake rate and/or aggression; a conclusion quite different from the one reached through multivariate analyses.

Second, the three response variables in our experiment were strongly correlated (Table 4). Multivariate analyses account for such correlations (Stevens 1996). It is also possible to account for correlations among the response variables in univariate analyses. In fact, this is what most published studies did: to statistically control for variation in forager abundance while studying treatments effects on intake rate and aggression, forager abundance was included as a covariate in analyses of covariance (ANCOVAs; Elgar 1987; Johnson et al. 2004, 2006) or as a predictor variable in regression analyses (Goldberg et al. 2001), abundance categories were defined (Balph 1977), or observations on higher abundances were excluded from the analyses (Cresswell 1997). All of these attempts to correct for variation in forager abundance are unwanted, because they distract attention from what may be the most important effect of the spatial distribution of food, a change in the abundance of foragers. In addition, several of these approaches, especially those that treat forager abundance as an independent variable, violate statistical assumptions. Use of ANCOVAs, for instance, assumes that the covariate itself is not affected by the treatment, and that the covariate is independent of the response variables (Underwood 1997). In most field experiments, the spatial distribution of food did affect the abundance of foragers. Also, that forager abundance would be independent of either intake rate or aggression is not at all obvious. Feedback effects of the rate of intraspecific interactions on the number of turnstones, are, for instance, quite likely, given that the prime reason of aggression may be to lower the number of competitors.

Third, use of multivariate statistics is to be preferred for reasons of conceptual clarity. Only multivariate analyses capture the experimental design correctly, treating as predictor variable that what has been experimentally manipulated (i.e. interpit distance) and treating as response variables that what has not (i.e. forager abundance, intake rate and aggression). Doing so helps to clarify the way experimental results are to be interpreted. Because multivariate analyses emphasize the uncontrolled nature of forager abundance, it becomes apparent that causal inferences on, for instance, the effect of forager abundance on aggression and/or intake rate cannot be made and that field experiments such as our experiment should be interpreted as patch choice experiments, even if there is only one experimental plot per trial. Alternative approaches, such as statistical control for correlations among response variables in univariate analyses, are apt to lead to confusion. Treating forager abundance as a predictor variable, for instance, requires assumptions on the causal relationships between forager abundance and aggression and/or intake rate. Also, it may give the false impression that after such control it is the causal relationships between interpit distance, intake rate and aggression

that can be studied. This, however, requires experimental, rather than statistical, control of forager abundance.

Implications

We found that the spatial distribution of food affects the combination of abundance, intake rate and aggression of free-living foragers. This finding is in agreement with the finding of laboratory experiments on captive animals that the spatial distribution of food affects interference (for a review, see [Vahl et al. 2005a](#)). Any more definite or quantitative statement on the effect of captivity cannot be drawn from comparisons between experiments on free-living foragers and the existing experiments on captive foragers. The fact that forager abundance is an experimentally controlled variable in experiments on captive animals and an uncontrolled response variable in experiments on free-living foragers makes these two kinds of experiments fundamentally different. In experiments in which forager abundance is experimentally controlled, it is the direct, causal effects of the spatial distribution of food on intake rate and aggression per se that can be studied. In experiments in which foragers abundance is not experimentally controlled it is the consequences thereof on the distribution of foraging animals over patches of food and the resulting relationships between the number of foragers, intake rate and aggression that can be studied. To link the two requires theoretical models, such as the ideal-free-distribution model, that predict the patterns that can be observed among free-living foragers on the basis of direct, causal relationships as determined in experiments on captive animals.

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Appendix: Analyses of Variance

To study whether univariate analysis of each of the three response variables would have led to different conclusions than the multivariate analysis, we reanalysed our data using ANOVAs on time spent digging (our measure of intake rate), on the rate of intraspecific interactions and on the number of turnstones, after log transforming each of these three response variables. In these ANOVAs, interpit distance (X) was included as a (categorical) treatment factor, and triplet as a (categorical) block factor. To facilitate comparison of conclusions with conclusions drawn in the main text, we used a 0.01 significance level in all tests.

We found that the distance between food pits had a significant effect on the number of turnstones on the experimental plots ($F_{2,17} = 66.5$, $P < 0.01$), but not on the intake rate of these turnstones ($F_{2,17} = 3.8$, $P = 0.04$), nor on their aggressive behaviour ($F_{2,17} = 3.2$, $P = 0.07$). The largest main effect on the number of turnstones was between the two smallest interpit distances; when food pits were 20 cm apart, more than three times as many turnstones were attracted by the same number of food pits and the same amount of food than when food pits were 10 cm apart (Fig. 1g). The intake rate of turnstones increased with the distances between food pits, but treatment averages did not differ significantly (Fig. 1e). Similarly, the rate of intraspecific interactions was lower when food pits were 30 cm apart than when they were 10 or 20 cm apart, but the overlap between treatments was substantial, and this effect was not statistically significant (Fig. 1f). The block factor triplet did not explain variation in any of these three responses (statistics not shown; Fig. 1e–g).

These findings would have corresponded to the results of Balph (1977) and Johnson et al. (2004, 2006), who found the number of foragers to increase with plot size, and to the results of Johnson et al. (2006), who reported plot size not to affect intake rate; they would have contradicted the finding of most field experiments that aggression decreases when food is spaced out (Table 1).